THE OLFACTORY LOBES, FORE-BRAIN, AND HABENULAR TRACTS OF ACIPENSER.

A SUMMARY OF WORK ON THEIR MINUTE STRUCTURE.[1]

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THE sturgeon of the Great Lakes, *Acipenser rubicundus*, Le Sueur, grows to a maximum length of about two meters. In my investigation I have used partly fish 25 to 40 cm. in length, and partly the smallest of the fish taken at the fisheries, 1 to 1½ meters in length. The greater part of the work has been done by the method of Golgi, although I have used the ordinary histological methods, and also methylene blue and acid fuchsin.

The form and relations of the fore-brain and olfactory lobes of Acipenser have been described and figured by Goronowitsch ('88). The figures accompanying the present paper illustrate the gross anatomy of these regions sufficiently well for an understanding of their minute structure. All the figures are from the brain of fishes 25 to 40 cm. in length.

A. *The Olfactory Lobe.*

In either transverse or longitudinal sections of the olfactory lobe three zones are easily distinguished (Fig. 1). These are, from without inward: the zone of olfactory fibers (*o.f.z.*), the zone of olfactory glomeruli (*gl.z.*), and the granular zone or zone of granule cells (*gr.z.*). The bundles of olfactory fibers spread out over the surface of the gray matter in such a way as to form a cap whose thickness is greatest at the anterior end and becomes *nil* near the junction of the olfactory lobe with the fore-brain. This zone is made up of intercrossed bundles of olfactory fibers with a small amount of connective tissue and a few pigment cells between them. The glomerular zone is char-

[1] From the Zoölogical Laboratory of the University of Michigan, Jacob Reighard, Director.

acterized, in preparations stained with haematoxylin, by the compact masses of branching dendrites and nerve fibers known as olfactory glomeruli. This zone constitutes about one-third of the thickness of the wall of the lobe. The granular zone is made up of numerous nerve cells and fibers. There is no distinct white zone. The axis cylinders of the cells of the lobe, as will be shown later, take the shortest course toward the fore-brain. In consequence, the granular zone is a mixed white and gray zone. It is readily distinguished from the glomerular zone, in ordinary preparations, by the absence of the glomeruli; but the line of division between the two zones is not sharply defined. The central cavity of the lobe is large and communicates widely with the cavity of the fore-brain (Fig. 1, *B*).

a. ZONE OF OLFACTORY FIBERS. — The fibers coming from the sense cells of the olfactory epithelium are gathered in bundles from 80 to 400 μ in thickness (Fig. 1, *o.f.z.*). The individual fibers differ considerably in thickness. They are very direct in their course and present definite varicosities at irregular intervals throughout their entire length. There is no evidence that the appearance of varicosities is due to imperfect impregnation, as suggested by Van Gehuchten and Martin (**'91**). (I learn from Miss Langdon that in her forthcoming paper on *Nereis virens* she will present evidence to show that such varicosities are artifacts.) The bundles break up into smaller bundles as they enter the gray matter.

b. ZONE OF OLFACTORY GLOMERULI. — The olfactory fibers approach their termination in the glomerular zone either in small bundles or singly. Occasionally the fibers divide shortly after entering this zone and end in two or more glomeruli, but the greater number divide only in the glomeruli in which they terminate. I shall consider the glomeruli after the various elements which may contribute to their formation have been described.

I have found in the glomerular zone three distinct forms of cells: mitral cells, stellate cells, and cells with short axis cylinders.

(1) There are present *mitral cells* of two varieties. The first (Fig. 1, *g*) are large, measuring from 16 to 48 μ in their short

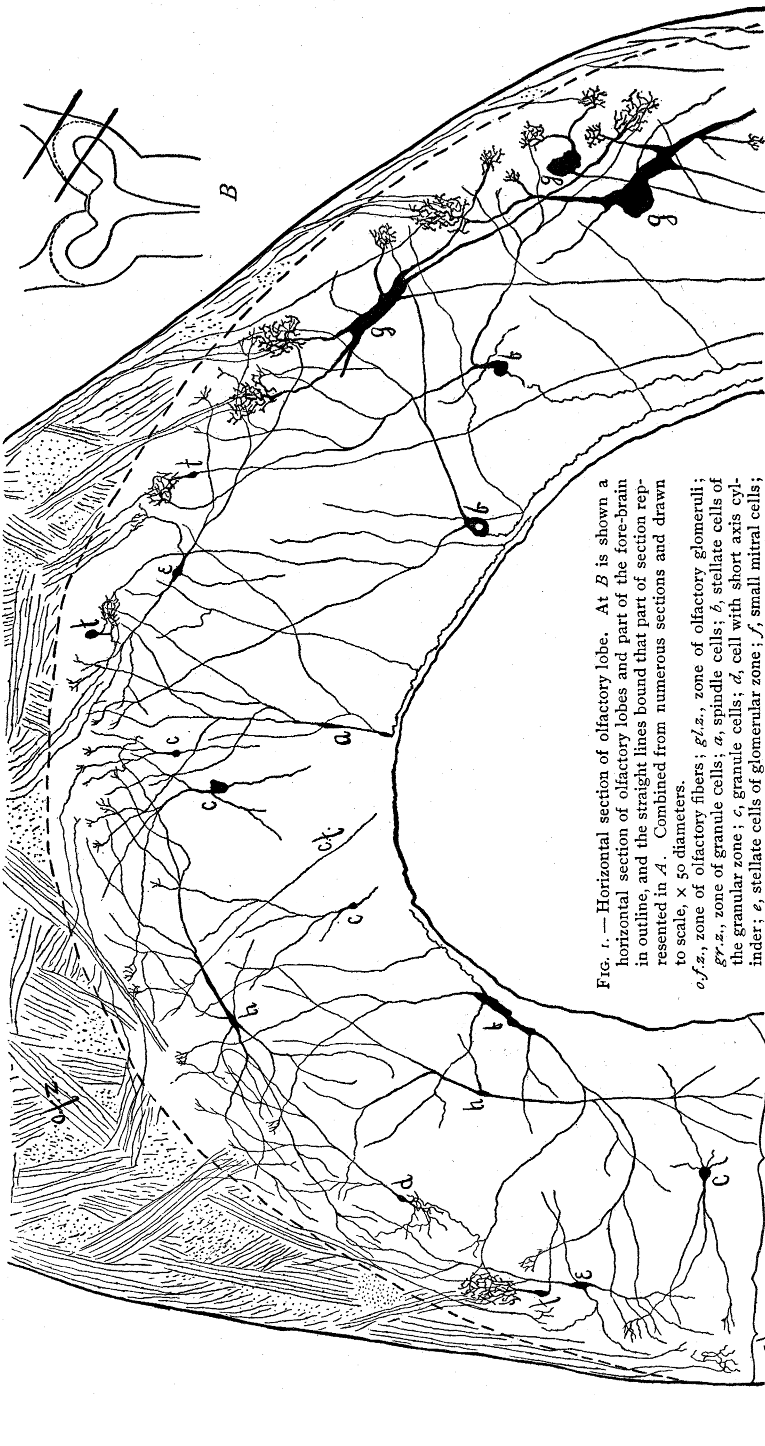


FIG. 1. — Horizontal section of olfactory lobe. At *B* is shown a horizontal section of olfactory lobes and part of the fore-brain in outline, and the straight lines bound that part of section represented in *A*. Combined from numerous sections and drawn to scale, × 50 diameters.

o.f.z., zone of olfactory fibers; *gl.z.*, zone of olfactory glomeruli; *gr.z.*, zone of granule cells; *a*, spindle cells; *b*, stellate cells of the granular zone; *c*, granule cells; *d*, cell with short axis cylinder; *e*, stellate cells of glomerular zone; *f*, small mitral cells; *g*, large mitral cells; *h*, cells of Cajal.

diameter and from 32 to 240 μ in their long diameter, possess from two to five thick dendrites, each of which supplies one or more olfactory glomeruli, and frequently have one or more slender dendrites which end freely in the glomerular zone without forming glomeruli. The axis cylinders are moderately thick fibers which take a direct course toward the fore-brain, and give off collaterals which rise toward the glomerular zone. The second variety of mitral cells (Fig. 1, *f*) are smaller, measuring 12 to 16 by 16 to 32 μ, have each a single thick dendrite which immediately breaks up into a glomerulus or into two or three imperfectly separated glomeruli, and have no non-glomerular processes. Their axis cylinders are usually directed centrally.

(2) *Stellate cells.* I have found numerous cells (Fig. 1, *e*) measuring 12 to 16 by 12 to 32 μ which have from two to five dendrites usually disposed parallel to the surface of the lobe, so that the cells have a stellate appearance in surface view. The dendrites are richly branched and long, their greatest expansion sometimes exceeding 1 mm. The branches of the dendrites end in olfactory glomeruli. The axis cylinders, which I have found in only a few cases, are directed either centrally or backward toward the fore-brain.

(3) The *cells with short axis cylinders* (Fig. 1, *d*) measure about 16 by 20 μ. From one end of the cell arises a thick dendrite whose branches end in glomeruli. A smaller process, which I take to be the axis cylinder, arises from the end of the cell opposite the dendrite and breaks up into numerous slender, smooth fibers which are lost in the glomerular zone. These cells are very few in number and very distinct in their character.

c. ZONE OF GRANULE CELLS. — Besides the granule cells which give this zone its name, I have found in it three other distinct forms of cells, which I shall call stellate cells, spindle cells, and cells of Cajal.

(1) The *stellate cells* (Fig. 1, *b*) measure 16 to 32 by 24 to 128 μ. They possess from three to five widely diverging dendrites whose branches end in the glomerular zone, where they enter into the formation of olfactory glomeruli. Their axis

cylinders are thick, strongly varicose fibers which run toward the central cavity of the lobe, and then along it close over or among the ependyma cells toward the fore-brain. From their horizontal portion the axis cylinders give off collaterals which branch once or twice in the outer part of the granular zone. They may enter the glomerular zone.

(2) The *spindle cells* (Fig. 1, *a*) measure 8 to 16 by 24 to 40 μ. The spindle-shaped cell body stands in a radial position in the internal one-third of the granular zone. From its peripheral end arises a dendrite whose branches end in olfactory glomeruli in the glomerular zone. From the central end of the cell a thick process runs toward the cavity and usually ends with an enlargement close to or among the bodies of the ependyma cells. From this enlargement an axis cylinder similar to those of the stellate cells runs backward to the fore-brain. Collaterals rise from it toward the glomerular zone. From the central process, and especially from its enlarged end, arise collaterals which branch and enter the glomerular zone. Sometimes the central process is without an enlargement, and it is perhaps to be regarded as part of the axis cylinder.

(3) The *granule cells* (Fig. 1, *c*) are numerous rounded or pyramidal cells measuring 8 to 32 μ in their greatest diameter. They occur at regular intervals throughout this zone. The character of these cells in other vertebrates has been much in dispute. Cajal in his earlier work ('90) considered them as certainly nervous, the peripheral process being the axis cylinder. Van Gehuchten and Martin ('91) are in doubt as to their character, having found no axis cylinder. Cajal later ('95) compares them with the spongioblasts of the retina, and considers them as nerve cells without axis cylinders. Koelliker ('96, pp. 709–713), on the other hand, regards them as certainly neuroglia. In Acipenser I have found these cells presenting characters showing them to be nerve cells conveying impulses from the olfactory fibers to the fore-brain. A description of them follows. Their peripheral processes rise to the glomerular zone and end in olfactory glomeruli; either forming, with olfactory fibers, glomeruli into which no other central elements enter, or entering glomeruli formed chiefly by other cells

described above. From the central end of the cell arises a slender, uniform, slightly varicose axis cylinder which runs either centrally or backward — that is, in the direction of all other axis cylinders. I have also found in some cases several short, slender dendrites arising from the central end of the cell about the base of the axis cylinder.

(4) *Cells of Cajal.* I have found at all levels of the granular zone very conspicuous elements (Fig. 1, *h*), measuring 8 to 20 by 24 to 40 μ, which in my earlier preparations seemed to correspond closely with certain cells with numerous axis cylinders described by S. Ramon y Cajal ('91) in the cortex of the rabbit, and afterward named by Retzius ('93) cells of Cajal. Later preparations brought to view in many of these cells characteristic end-branchings of some of the processes in olfactory glomeruli, and a single distinct axis cylinder arising from the cell body or from one of the thick processes and running centrally and backward toward the fore-brain. These cells, therefore, like all others of the olfactory lobe except those with short axis cylinders, receive impulses from olfactory fibers and transmit those impulses to the fore-brain. It seems probable, however, that some of the dendrites do not end in glomeruli, and that such dendrites may receive impulses from many collaterals and so serve as important parts of the collateral paths. Since coming to the above conclusions there has come to my notice the recent paper of Veratti ('97) criticising Cajal's interpretation of the cells in the rabbit's cortex and announcing that each cell has a single true axis cylinder. My account agrees with that of Veratti, and I have therefore called the cells here described cells of Cajal.

In addition to the elements described above, I have found in a very few cases fibers ending freely in the glomerular zone (Fig. 1, *c.f.*) which probably correspond to the centripetal fibers of Golgi ('75) and S. Ramon y Cajal ('90).

The olfactory glomeruli do not differ in general appearance from those described by S. Ramon y Cajal, Van Gehuchten and Martin, Koelliker, Retzius, Loewenthal, P. Ramon y Cajal, and others in mammals, birds, reptiles, and amphibia. In Acipenser the glomeruli vary in diameter from 16 to 240 μ, and

are much more complex than in mammals. They may receive from two or three to a large number of olfactory fibers, and the size of the glomerulus is probably determined by the number of olfactory fibers entering it. Each glomerulus may be supplied by a single large or small bundle of fibers, or by several single fibers or small bundles of fibers coming, it may be, from widely separated bundles of the olfactory nerve. Each olfactory fiber usually has from two to five end-twigs produced by dichotomous divisions, but frequently the branching is irregular, and it may be very complex. I have found no indication of anastomosis or the formation of a network in these endings. To the central portion of the glomerulus dendrites may be contributed by any one or several of the eight forms of cells described above. The largest part of a typical glomerulus is formed by the end-branching of the mitral cell dendrites, but almost all the glomeruli in Acipenser are formed in part by the dendrites of other cells. The whole makes up a very complicated mass of interwoven nerve twigs among which ramify the processes of glia cells. The essential condition for the transference of nerve impulses in the glomerulus is the contact of the tips of the olfactory fiber end-branches with the dendrites. There is in Acipenser no evidence of continuity of nerve substance between olfactory fibers and dendrites. Besides these typical glomeruli, there are many small ones whose central portion is formed wholly by the dendrites of cells other than the mitral cells.

I have thus recognized eight forms of nerve cells in the olfactory lobe. On the whole, these cell forms are distinct and present well-marked characters. However, there are to be found occasional intermediate forms: between the cells *a* and *c*, *b* and *c*, *b* and *e*, *c* and *f* (Fig. 1). Only the large and small mitral cells (and the granule cells ?) can with certainty be compared with cell forms heretofore described in other vertebrates. The olfactory lobe of other fishes (especially Cyclostomes and Elasmobranchs) and of Amphibia needs to be investigated by the Golgi method and the lobe of higher vertebrates reëxamined with reference to the occurrence of the other cell forms. The only work done by modern methods on the olfactory lobe of

fishes hitherto is that of Van Gehuchten ('**94**) on the trout and that of Sauerbeck ('**96**) on Elasmobranchs. Van Gehuchten gives a single small figure of the end-branching of several olfactory fibers, and Sauerbeck states that he has had a few olfactory glomeruli and mitral cells impregnated, but gives no figure. In the frog I have found stellate cells similar to those in the granular zone of Acipenser, their axis cylinders directed toward the fore-brain. Similar cells, but devoid of axis cylinders, are shown in a figure copied by Edinger ('**96b**, p. 142) from a paper by P. Ramon y Cajal ('**94**) which I have not seen. The question of the interpretation of the various forms of nerve cells in the olfactory lobe of vertebrates I am not yet prepared to discuss.

S. Ramon y Cajal ('**96a**) makes use of the mitral and granule cells of the olfactory lobe to illustrate his principle that a nerve cell gains a higher morphological development by the growth of new processes, which by their position and direction set up connections with a greater number of cells. Interpreted by this statement, the large mitral cells of Acipenser present as high a stage of differentiation as those of mammals, or higher. The dendrites of these cells supply several, usually large glomeruli, into which a very large number of olfactory fibers enter. Thus the number of cells with which they come into relation is greater than in mammals. I have now shown also that non-glomerular protoplasmic processes which were hitherto unknown in lower vertebrates are present in Acipenser. With regard to the granule cells, if centrally directed axis cylinders should be found in higher vertebrates, all previous interpretations of them will fall to the ground. Here, again, the presence of basal processes goes to show that the morphological distinction between nerve cells in fishes and mammals is not so great as previous work has led us to suppose.

B. *The Fore-Brain.*

a. GENERAL DESCRIPTION OF NUCLEI AND FIBER TRACTS. — In sections stained with methylene blue and acid fuchsin or with haematoxylin there are to be seen several distinct collections of

cells whose size and position I shall briefly indicate (Figs. 2–4). First is the large dorsal and median portion bulging into the central cavity and constituting about one-half of the entire fore-brain. It is the corpus striatum. At the anterior end, near the border of the olfactory lobe, are two compact groups of cells, one ventral and median and one lateral, which together make up the lobus postolfactorius. I shall refer to these nuclei as the ventral and lateral nuclei postolfactorii (Fig. 2). Over the greater part of the lateral surface of the fore-brain are scattered small cells whose character I have not yet certainly determined. I shall describe this area under the name of the cortex (Fig. 3). The cells immediately surrounding the ventral portion of the cavity of the fore-brain behind the anterior commissure together with those surrounding the recessus praeopticus form a distinct nucleus which corresponds with the nucleus thaeniae of Edinger (**'96a**).

Three main fiber tracts are to be mentioned here (Figs. 2–4). The large number of fibers entering the fore-brain from the olfactory lobe constitute a tractus olfactorius, although so short as not to appear in the gross anatomy of the brain. More conspicuous is the large bundle of fibers traversing the ventro-lateral portion of each half of the fore-brain and entering the 'tween-brain, the tractus strio-thalamicus. A smaller bundle connects the fore-brain with the Ganglion habenulae, the tractus olfacto-habenularis. In addition to these longitudinal tracts is the large anterior commissure connecting the two halves of the fore-brain at about the middle of their length.

b. Histology of the Several Nuclei. — (1) The *corpus striatum.* The striatum contains two distinct types of cells imperfectly separated into two nuclei. The internal (dorso-median) nucleus (Figs. 2, 3, *Epistriatum*) is composed of pyramidal cells measuring 12 to 26 by 16 to 40 μ arranged in about ten to twelve compact layers parallel with the internal surface of the striatum. The apices of the cells are directed latero-ventrad. Each cell has several basal processes, and from the apex arise from one to four dendrites which are marked by characteristic spiny projections described by Van Gehuchten (**'94**)

for the cells of the fore-brain of the trout. The axis cylinders arise from the side or apex of the cell body or from the first portion of one of the basal or apical dendrites. Each fiber is of medium thickness and quite smooth. It runs latero-ventrad, grows distinctly more slender as it is traced further from the

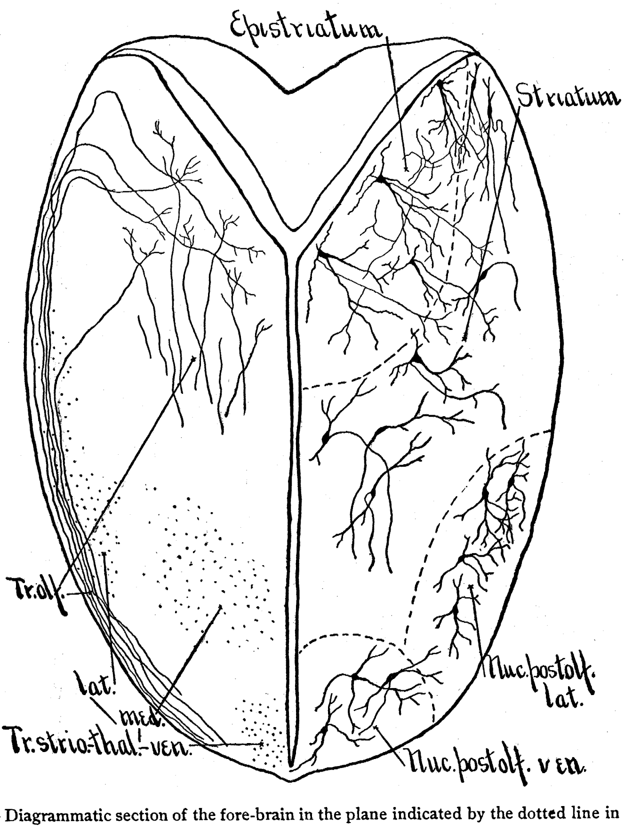


FIG. 2. — Diagrammatic section of the fore-brain in the plane indicated by the dotted line in Fig. 4, *a*. Outline, × 25 diameters; cells, × 50 diameters.

cell, gives off numerous collaterals which ramify widely in the striatum, and ends with terminal branches in the external portion of the striatum. All my preparations contain many cells of this sort.

The external nucleus (Figs. 2, 3, *Striatum*) is composed of irregular cells with two or more dendrites, which are not arranged in layers and are not so compactly grouped as are those of the internal nucleus. The cells measure 12 to 24 by

12 to 48 μ. The dendrites present the same appearance as those of the pyramidal cells. The axis cylinders arise from the cell bodies or from the basal part of the dendrites, are medium-sized, smooth fibers of uniform diameter, give off few and short or no collaterals, and enter the tractus strio-thalamici. Many cells of this description are scattered among the pyramidal cells of the internal nucleus and some of them have a pyramidal form, so that it is sometimes difficult to distinguish between

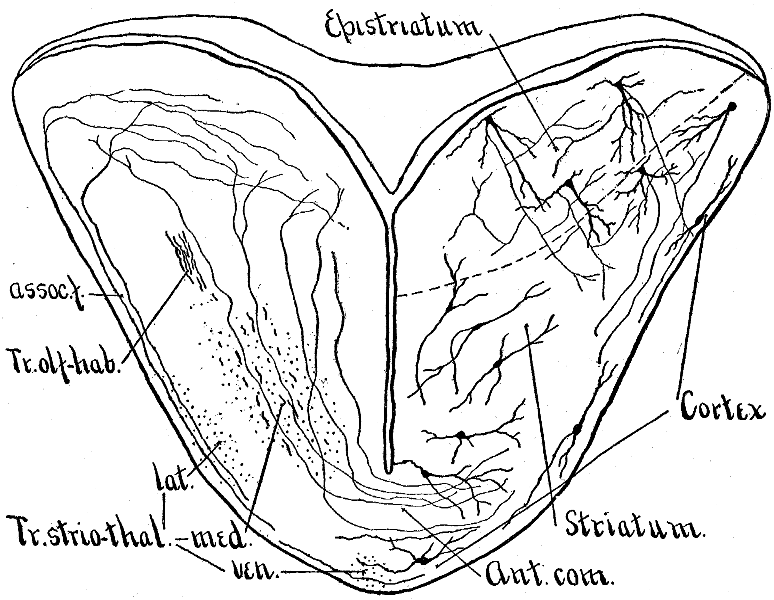


FIG. 3. — Diagrammatic frontal section of the fore-brain through the anterior commissure. Scale as in Fig. 2.

the two types of cells. In a single series in which the axis cylinders are very well impregnated, I have in a few cases found the two kinds of cells side by side in the same section. It should be added that the cells in the ventral part of the striatum are smaller, have usually only two dendrites, send their axis cylinders into the median portion of the tractus strio-thalamici, and are readily distinguished from the pyramidal cells of the internal nucleus.

Goronowitsch ('88) describes the appearance of these two nuclei in picrocarmine preparations of the brain of *Acipenser ruthenus*. Van Gehuchten ('94) states that in the trout all the

cells impregnated in his preparations are multipolar with axis cylinders entering the tractus strio-thalamici (basal bundles of Edinger's earlier work). He does not mention or figure collaterals. Either the pyramidal cells with short axis cylinders described above for the internal nucleus were not impregnated in his preparations, or from seeing the axis cylinders directed toward the basal bundle he has concluded that they join it. Whether the cells with short axis cylinders described above are the same as those referred to by Van Gehuchten ('**94**) as having been described by Bellonci in teleosts ('**79** ?) I cannot tell, as I have not had access to Bellonci's paper. In a single case I have found a small cell in the intermediate portion of the striatum with two dendrites and with short axis cylinder disposed longitudinally.

The fibers having their endings in the corpus striatum come from two or three sources: the olfactory lobe, the thalamus, and probably the cortical area. The fibers from the olfactory lobe which pass into the corpus striatum are best seen in such a section as that represented in Fig. 2 (*tr. olf.*). These fibers end, so far as I have seen, only in the internal nucleus of the corpus striatum. The fibers entering the corpus striatum from the thalamus (Fig. 4, *D*) are the ascending or sensory fibers described by Van Gehuchten ('**94**) in the Tractus strio-thalamici (basal bundles) of the trout. Probably the greater number of these fibers cross in the anterior commissure (Fig. 3, *ant. com.*), but some seem to find endings on the same side. They are fine or medium-sized varicose fibers which end by fine ramifications in the internal nucleus of the corpus striatum. I have not found their endings in the external nucleus. In addition to the fibers last mentioned, the anterior commissure contains a small number of thick, strongly varicose fibers which course around the lateral surface of the fore-brain and enter the corpus striatum at its dorso-lateral angle (Fig. 3, *assoc. f.*). Either before or after entering the corpus striatum these fibers break up into several very fine branches which run for a long distance in the internal nucleus parallel with its layers of cells. These fibers will be described below as the probable axis cylinders of the cells of the cortex.

The two nuclei of the corpus striatum described above are not sharply differentiated. Since the fibers from the tractus olfactorius are found to end in the internal nucleus and have not been seen to end elsewhere in the striatum, this nucleus is probably homologous with the epistriatum as described by Edinger ('96a, b) in reptiles, amphibia, and teleosts. The cells of the external nucleus give rise to descending fibers of the tractus strio-thalamici, and are therefore to be considered as the motor component of the corpus striatum. In the intermediate portion there is a mingling of cells of the two kinds, and hence a region of mixed functions. It seems probable that the epistriatum consists properly of the cells with short axis cylinders, here not fully separated from the striatum, and that they receive all sensory and associational impulses (*e.g.*, from the three sources indicated above), and in turn stimulate the motor cells which constitute the striatum proper.

(3) *Nuclei postolfactorii.* The nucleus postolfactorius ventralis, occupying the ventro-median angle of the fore-brain at its extreme anterior end, is made up of multipolar and bipolar cells. The multipolar cells measure 12 to 16 by 16 to 26 μ. They have irregularly spreading dendrites. From the cell body arises a medium-sized smooth axis cylinder which is directed backward along the ventral surface of the fore-brain, near the median line. The bipolar cells have bodies measuring 16 to 17 by 16 to 32 μ. From each end of the cell arises a thick dendrite directed parallel with the long axis of the brain. The dendrites give off several small branches at right angles. The posteriorly directed dendrite gradually becomes transformed into a thick, varicose axis cylinder, which I have traced more than half the length of the fore-brain. The axis cylinders of both multipolar and bipolar cells traverse the length of the fore-brain, forming a small bundle at each side of the mid-ventral line, pass among the cells surrounding the recessus praeopticus, and pierce the large bundles of the optic nerve. I have not yet certainly determined their place of ending (Fig. 4, *B*). The fibers which enter and end in this nucleus come from the olfactory lobe. Most or all of them are fibers which run close over the central cavity; hence, probably, the axis cylin-

ders of the stellate and spindle cells of the granular zone. The terminal branches are thickened and varicose.

The nucleus postolfactorius lateralis is much larger than the ventralis. It is made up of multipolar cells similar to those of the ventralis, measuring 16 to 20 by 20 to 24 μ. Their axis cylinders, together with fibers from the anterior end of the striatum, form a bundle of fibers which runs ventro-posteriorly over the lateral surface of the fore-brain (Fig. 4, *C*). At the optic thalamus the bundle turns mesad, plunges through some of the more mesial optic bundles, and continues into the 'tween-brain with the tractus strio-thalamicus medius, on the lateral surface of which it forms a distinct bundle. Its destination I have not yet worked out. The fibers which end in the lateral nucleus postolfactorius come from the olfactory lobe, but from what cells of the lobe I cannot at present say. They seem to be those axis cylinders which take the most direct course to the fore-brain and do not run close over the central cavity; hence, some of the axis cylinders of the granules, the cells of Cajal, the mitral cells, and the stellate cells of the glomerular zone.

There seems to be a third nucleus occupying the antero-dorsal angle of the fore-brain having relations similar to those of the lateral nucleus. Since its cells have been impregnated in only a single series, I cannot describe it further. It may be a nucleus postolfactorius dorsalis, or it may belong to the epistriatum.

In addition to the fibers which run from the nuclei postolfactorii to the ventral portion of the 'tween-brain, there are several small bundles of fibers which connect these nuclei with the ganglia habenulae. Tracing the fibers forward from the ganglion of habenula, the bundle breaks up in the posterior dorsal portion of the fore-brain into several small bundles, which diverge like the ribs of a fan and penetrate to the ventral part of the fore-brain *throughout its entire length.* Here I have been unable to find either terminal arborizations or cells of origin, owing in some cases to imperfect impregnation and in others to the great number of fibers of other tracts, making it impossible to trace these through successive sections. How-

ever, in the ganglia habenulae the fibers in question cross to the opposite side through the commissura habenularis and seem to end by free branching among the dendrites of the cells which give rise to the bundles of Meynert. This renders it probable that these fibers constitute the tractus olfacto-habenularis (Fig. 3, *Tr. olf.-hab.;* Fig. 4, *E*).

I will here insert a note on the course of the bundles of Meynert as throwing light on the function of the olfactory nuclei as well as on that of the ganglia habenulae. For these conspicuous bundles traversing the internal faces of the walls of the 'tween-brain I have not adopted the name proposed by Edinger,—tractus habenulo-peduncularis,—for the reason that in Acipenser their fibers do not end in the corpus interpedunculare as described by Mayser ('82), Van Gehuchten ('94), Edinger ('96b), and S. Ramon y Cajal ('96b) for other forms. In the corpus interpedunculare a majority of the fibers of the bundles of Meynert cross to the opposite side, and both the crossed and uncrossed fibers pass on back toward the medulla. I have not traced them to their endings. I give a figure (Fig. 5) of the course of the fibers through the corpus interpedunculare.

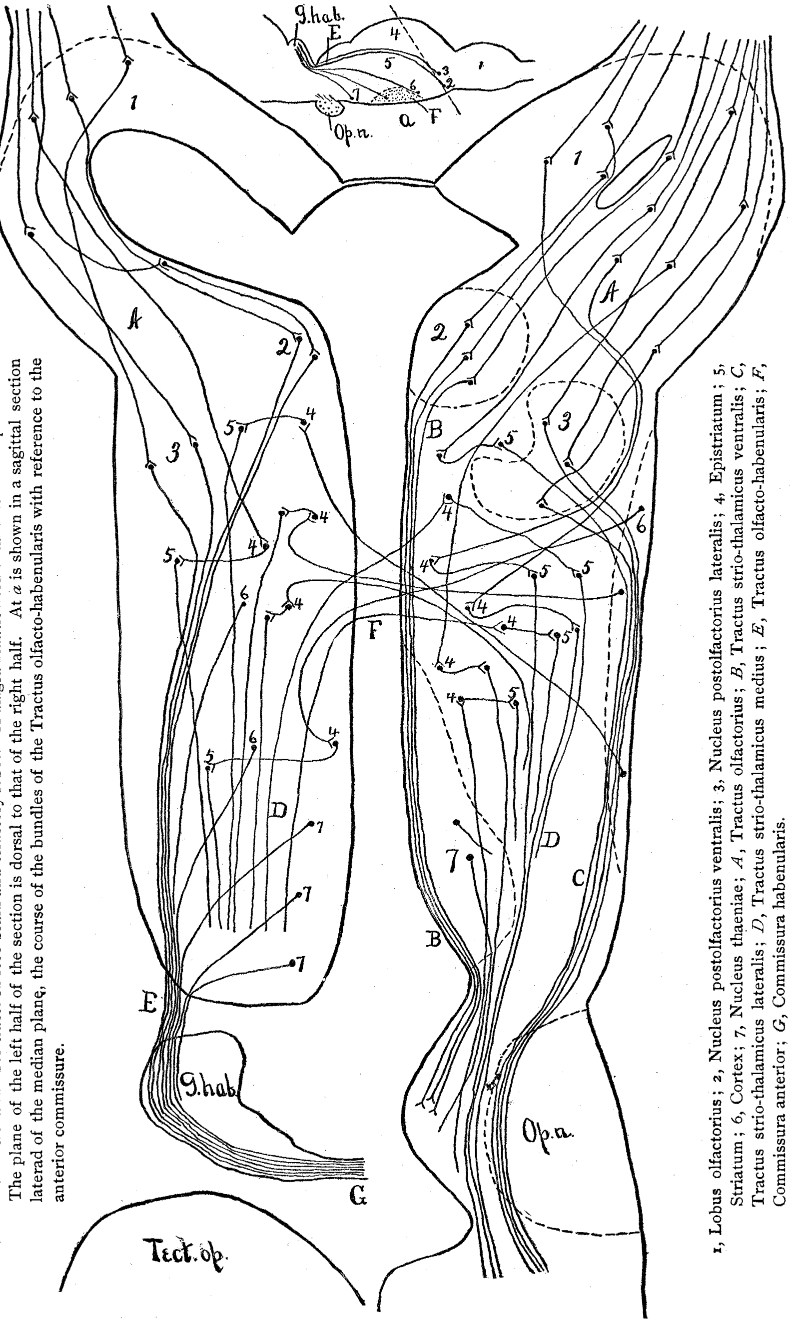
(4) *The cortex.* Among the fibers from the lateral nucleus postolfactorius and striatum on the lateral and ventral surfaces of the fore-brain occur cells measuring 12 to 18 by 16 to 40 μ with two or more dendrites usually disposed parallel with the external surface (Fig. 3). In the anterior commissure are found a small number of thick fibers with very definite, round varicosities at regular intervals (Fig. 3, *assoc. f.*). In a few cases I have found the axis cylinders arising from the superficial cells just mentioned directed toward the anterior commissure and having the characters of these thick fibers. Tracing the fibers, they are found to end in the epistriatum in the manner described above. Some of the cells of this region have very slender, smooth axis cylinders directed toward the anterior commissure. I have been unable to trace them to their destination. The fibers which end among these cells are collaterals from the axis cylinders of striatum cells, occasional short axis cylinders from the epistriatum, and probably fibers from the tractus olfactorius.

It seems probable that at least some of the cells here described are associational cells serving to coördinate the motor impulses descending from the two halves of the fore-brain, while other cells may belong to the olfactory area and give rise to a part of the tractus olfacto-habenularis. The disposition of the bundles of the tractus olfacto-habenularis, to be noted below, suggests homology of the cells just described with the cortex lateralis of reptiles, to which they correspond in position. In the choroid roof of the fore-brain in Acipenser I have had one or two nerve cells and fibers impregnated in a few preparations. These cells correspond in position with the cortex dorsalis of higher forms.

(5) *Nucleus thaeniae.* The cells surrounding the recessus praeopticus and the ventral portion of the central cavity of the fore-brain as far forward as the anterior commissure constitute a nucleus corresponding to the nucleus occipito-basalis of Herrick ('91) and the nucleus thaeniae of Edinger ('96a). Their dendrites spread widely toward the lateral surface of the fore-brain. At least some of their axis cylinders run backward through the optic chiasma; I have been unable thus far to trace them to their endings. There is a decussation of some of the fibers beneath the recessus praeopticus. It may be that this is an important olfactory nucleus, but I have been unable to trace any fibers to it from the olfactory tract. It would be impossible, however, to trace such fibers if they were present in my preparations, owing to the enormous number of other fibers among which they must run. There is some evidence that this is an olfactory nucleus in the fact that some bundles of the tractus olfacto-habenularis arise from this region, probably from some of the cells of the nucleus thaeniae here described.

c. THE FIBER TRACTS. — Under this head I collect the statements scattered through the preceding pages and make some additions to them.

(1) The tractus olfactorius is for the most part very diffuse. The great majority of its fibers enter the fore-brain singly and are at once mingled with the fibers of other tracts. Only a small part of its fibers are gathered into a compact bundle.



Scheme of nuclei and fiber tracts in fore-brain and olfactory lobes. A diagrammatic horizontal section is represented. The plane of the left half of the section is dorsal to that of the right half. At *a* is shown in a sagittal section laterad of the median plane, the course of the bundles of the Tractus olfacto-habenularis with reference to the anterior commissure.

1, Lobus olfactorius; 2, Nucleus postolfactorius ventralis; 3, Nucleus postolfactorius lateralis; 4, Epistriatum; 5, Striatum; 6, Cortex; 7, Nucleus thaeniae; *A*, Tractus olfactorius; *B*, Tractus strio-thalamicus ventralis; *C*, Tractus strio-thalamicus lateralis; *D*, Tractus strio-thalamicus medius; *E*, Tractus olfacto-habenularis; *F*, Commissura anterior; *G*, Commissura habenularis.

Fig. 4.

This bundle is formed in the ventral part of the olfactory lobe, enters the fore-brain through the nucleus postolfactorius ventralis, courses round the lateral surface of the nucleus postolfactorius lateralis, and enters the epistriatum at its dorso-lateral angle (Fig. 2). I have traced olfactory tract fibers into the epistriatum and into the two nuclei postolfactorii. I have been unable to trace any fibers between the anterior commissure and the olfactory lobe. Although we might expect to find olfactory tract fibers ending in the nucleus thaeniae and in the area described as cortex, I have been unable to trace them to either with certainty.

(2) The tractus strio-thalamicus, considered as including all fibers connecting the fore-brain with the ventral portion of the 'tween-brain, is divided into three portions: the median, lateral, and ventral bundles. The median bundle is much the largest, and occupies the position indicated in Figs. 2, 3 (*Tr. strio-thal. med.*), and 4 (*D*). It contains the descending axis cylinders of the cells of the striatum and the ascending fibers from the thalamus to the epistriatum. The lateral bundle (Figs. 2 and 3, *Tr. strio-thal. lat.*, and Fig. 4, *C*) contains fibers arising from the nucleus postolfactorius lateralis and from the anterior part of the striatum. Its course has been described. The ventral bundle (Figs. 2 and 3, *Tr. strio-thal. ven.*, and Fig. 4, *B*) consists only of fibers from the nucleus postolfactorius ventralis whose course has been described above.

(3) The tractus olfacto-habenularis (Fig. 4, *E*) arises from cells of the nuclei postolfactorii and probably from cells of the cortical area and of the nucleus thaeniae, and passes to the ganglion habenulae where most or all the fibers cross to the opposite side to end among the dendrites of the cells giving origin to the bundles of Meynert. That the bundles here described are equivalent to more than Edinger's tractus olfacto-habenularis is shown by their relation to the anterior commissure. The tract to which Edinger gives this name arises in the ventrally situated nucleus thaeniae and area olfactoria and runs behind and below the anterior commissure (see Edinger, '96a, p. 343, Fig. 5, or '96b, p. 148, Fig. 100), while the larger part of the fibers here included under that name arise in the

nuclei postolfactorii (and cortex?) and run in front of and above the anterior commissure. It is probable that this portion includes Edinger's tractus cortico-habenularis. The bundles in Acipenser from the nuclei postolfactorii do not seem to be represented in Edinger's scheme.

(4) The bundles of Meynert arise from cells in the ganglia

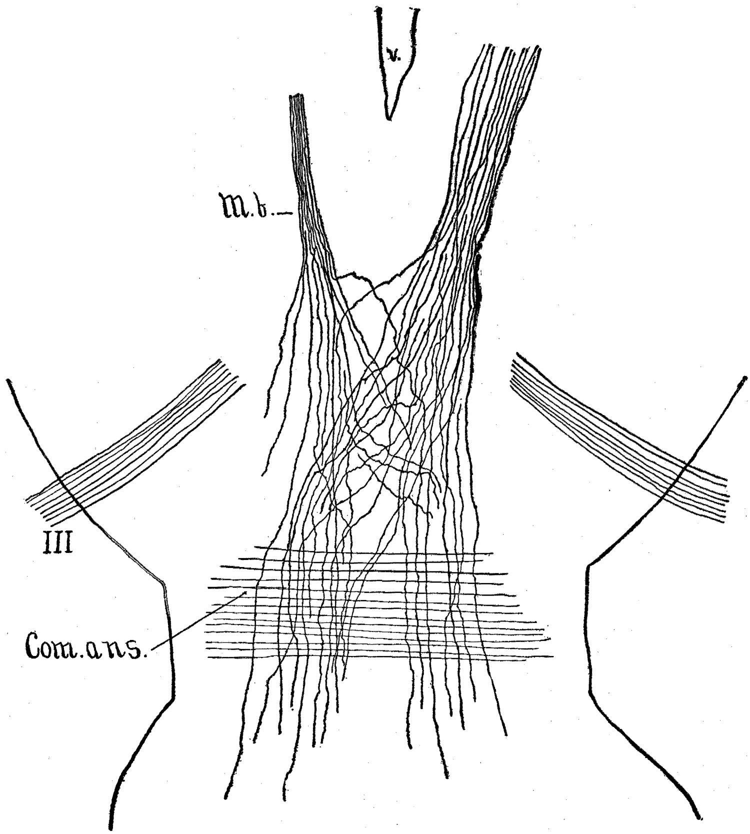


Fig. 5. — Frontal section through region of Corpus interpedunculare, showing decussation of Meynert's bundles. *M.b.*, Meynert's bundles; *III*, Nervus oculomotorius; *Com. ans.*, Commissura ansiformis; *v.*, cavity of mid-brain. Camera drawing.

habenulae as described by Van Gehuchten ('94) in the trout, traverse the walls of the 'tween-brain to the region of the corpus interpedunculare in the base of the mid-brain, thence, after decussation of most of the fibers, pass back toward the medulla. Other habenular tracts will be described in my final paper.

(5) The anterior commissure is made up chiefly of ascending fibers which cross to end in the epistriatum of the opposite side. In addition to these are the somewhat doubtful associational fibers of the cortical area, crossing likewise to terminate in the epistriatum.

Summary of Results.

A. The olfactory lobe:

(1) In addition to mitral cells of two sorts, six other forms of cells, concerned in receiving and transmitting olfactory impulses, are found in the olfactory lobe.

(2) The granule cells are provided with axis cylinders and glomerular dendrites, and are therefore nerve cells.

(3) The olfactory lobe contains cells which are morphologically identical with the cells of Cajal.

(4) The glomerular zone of the olfactory lobe contains cells with short axis cylinders (associational cells).

(5) The large mitral cells are provided with non-glomerular dendrites.

B. The fore-brain:

(6) There is in the dorso-median region of the fore-brain a large incompletely differentiated nucleus of cells with short axis cylinders, constituting an imperfect epistriatum.

(7) A group of cells is found on the lateral surface of the fore-brain which agrees in position and apparently also in connections with the cortex lateralis of *Reptilia.*

(8) The cortical region of the fore-brain is connected with the ganglion habenulae by a tractus cortico-habenularis. A tractus olfacto-habenularis is also present.

C. The habenular tracts:

(9) Meynert's bundles do not end in the corpus interpedunculare, but undergo partial decussation there and pass on toward the medulla.

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